



# Optimal synchrony state for maximal information transmission

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This work investigated the roles of spontaneous synchronized rhythmic oscillations in information processing in a globally coupled neural network. We found that in the encoding of input aperiodic signals, there exists a range of optimal synchronous states in the network, where the information transmission rate

and coding efficiency of the network are maximized. Our results indicate that it is not the weaker and stronger but an appropriate synchronous state may be of more functional significance in sensory encoding. *NeuroReport* 15:000–000 © 2004 Lippincott Williams & Wilkins.

**Key words:** Coding efficiency; Information transmission; Stochastic resonance; Synchrony

## INTRODUCTION

Synchronous activities in neuronal ensembles are ubiquitous phenomena observed in many regions of the brain using multi-electrode recording techniques [1,2]. There have been intense efforts to study the mechanisms of their generation [3] and their functional roles [1–3]. These studies suggested that synchronized rhythmic oscillations, especially  $\gamma$ -band oscillations (with frequencies in the range of 30–70 Hz) [4] may play important roles in a variety of top-down cognitive processes such as perception, memory, selective attention, binding, and gain control. However, their roles in the processing of sensory information have not been clearly clarified, especially when considering that neurons are bombarded with random synaptic inputs.

Neurons do function well in a noisy environment [5]. There are a lot of studies concerning how neurons obtain high accuracy and efficiency in the coding of signals in such a noisy environment and how neurons communicate with one another in a noisy background. Population coding and synchrony might be important in making information encoding and transmission robust in a noisy environment [2,6]. A pool of uncoupled neurons processing identical input can behave as a more robust computational unit against random noise [6]: their average activities serve to provide instantaneous firing rate as well as to average out random uncorrelated noise. When neurons in the pool are coupled together, their activities become more synchronous and correlated. The correlation and synchrony may enhance the selectivity of preferred signals [7], temporal fidelity in the encoding of information and robustness against noise at the cost of reducing information coding capacity [8]. Strong empirical evidences exist in support of these ideas [1,2,7,8].

Modeling studies [9,10] indicated that neurons in the coupled network could become more entrained to the inhibitory drive, leading to a more efficient information transmission by spike timings. Moreover, cortical neurons are found more sensitive to synchronous than to asynchronous input [11]. Synchronous input can trigger precise spiking patterns [11], which can be propagated stably through cortical networks [12]. Thus, synchrony in a population of neurons, on the one hand, tends to reduce spike variability and increase coding redundancy with the net effect of reducing the aggregate capacity of information encoded by the network [13]. On the other hand, synchrony introduces correlation, enhances the selection, communication, information transmission, and coding accuracy against large noise disturbances [7–10]. Considering the positive and negative roles of synchronous activities discussed above, there may exist a tradeoff where information encoding process could be optimized. In this report, we explore the ways in which synchrony can enhance information processing in a noisy neural network.

The effect of noise is not always deleterious. An appropriate level of noise in the input can facilitate the processing of weak signals in a non-linear system by a mechanism called stochastic resonance (SR; for review see [14]). Neurons possess the essential dynamical features such as excitability, threshold and saturation, which allow them to manifest SR phenomenon. Numerous experiments revealed evidence of SR in nervous systems [14]. Recent studies also indicated that optimal noise level inside the coupled network might help to generate spontaneous synchronized activity [15]. These spontaneous activities can sharpen heavily the frequency tuning curve of the

network thus increasing greatly the signal-to-noise ratio (SNR) to the preferred periodic signals [15]. However, natural signals always fluctuate and are aperiodic, and how the spontaneous activities affect neural coding of aperiodic signals is unclear and has attracted great attention. We attempt to clarify this issue in this report, which might shed a light on the debate whether the synchrony is merely an epiphenomenon of biological neural networks [13].

## MODEL AND METHODS

Let us consider a network composed of Hodgkin-Huxley (HH) neurons [16], globally coupled via excitatory synapses,

$$C_m \dot{V}_i = -g_{Na} m_i^3 h_i (V_i - V_{Na}) - g_K n_i^4 (V_i - V_K) - g_l (V_i - V_l) + I_i^{Noise} + s(t) + I_i^{syn}(t), \quad (1)$$

$$\dot{m}_i = [m_\infty(V_i) - m_i]/\tau_m(V_i), \quad (2)$$

$$\dot{h}_i = [h_\infty(V_i) - h_i]/\tau_h(V_i), \quad (3)$$

$$\dot{n}_i = [n_\infty(V_i) - n_i]/\tau_n(V_i), \quad i = 1, \dots, N. \quad (4)$$

$V_i$ ,  $m_i$ ,  $h_i$  and  $n_i$  are the membrane potential, the gating variables of  $Na^+$  and  $K^+$  channels, respectively.  $g_{Na}$ ,  $g_K$  and  $g_l$  are the maximal values of conductance of the sodium, potassium, and leakage currents;  $V_{Na}$ ,  $V_K$  and  $V_l$  are the corresponding reversal potentials. The membrane capacitance is  $C_m = 1 \mu F/cm^2$ . The number of neurons  $n = 1000$ . The auxiliary functions and the parameter values can be found in the references [16].

Each neuron receives three types of input in the network: (1)  $I_i^{Noise}$  represents the noisy component of the synaptic current to a neuron from external fluctuations or intrinsic fluctuations of the neuron itself,

$$I_i^{Noise} = I_0 + \xi_i(t), \quad (5)$$

where  $I_0$  is the mean value of the background fluctuations, while  $\xi_i(t)$  is independent Gaussian white noises with  $\langle \xi_i(t) \rangle = 0$  and  $\langle \xi_i(t_1) \xi_j(t_2) \rangle = 2D \delta_{ij} \delta(t_1 - t_2)$ . Here, we let  $I_0 = 1 \mu A/cm^2$  and keep invariant in all the situations. (2)  $s(t)$  is the external input signal (periodic or aperiodic). (3) The synaptic current from coupling among the network was described by [17].

$$I_i^{syn} = - \sum_{j=1, j \neq i}^N \frac{g_{syn}}{N} \alpha(t - t_j) (V_i - V_{syn}^{ij}), \quad (6)$$

with

$$\alpha(t') = \frac{t'}{\tau_s} e^{-t'/\tau_s}, \quad (7)$$

where  $t' = t - t_j$ , and  $t_j$  is the firing time of the  $j$ th neuron;  $\tau_s = 2$  ms is the characteristic time of the synaptic interactions,  $V_{syn}^{ij}$  is the synaptic reversal potential taken as 30 mV [17], and  $g_{syn}$  is the coupling strength.

The spike trains of each neuron are recorded and converted into binary sequences with a time bin equal to 2 ms, 0 representing non-firing and 1 representing firing state. The numerical integration of the equations described above is performed by a second-order stochastic algorithm [18]. The integration step is taken to be 0.01526 ms.

To quantify the synchronization of neuronal firings in a network, we use a coherence measure [19] based on the

normalized cross-correlations of neuronal pairs in the network. The coherence between two neurons  $i$  and  $j$  is measured by their cross-correlation of spike trains at zero time lag within a time bin of  $\Delta t = \tau$ . Suppose that a long time interval  $T$  is divided into small bins of  $\tau$  and that two spike trains are given by  $X(l) = 0$  or 1,  $Y(l) = 0$  or 1, with  $l = 1, 2, \dots, K$  (here  $T/K = \tau$ ), respectively, then a coherence measure for the pair is defined as

$$k_{ij}(\tau) = \frac{\sum_{l=1}^K X(l)Y(l)}{\sqrt{\sum_{l=1}^K X(l) \sum_{l=1}^K Y(l)}}. \quad (8)$$

Here,  $\tau$  is taken to be 2 ms. Furthermore, a population coherence measure  $k$  is defined by the average of  $k_{ij}(\tau)$  over all pairs of neurons in the network, that is

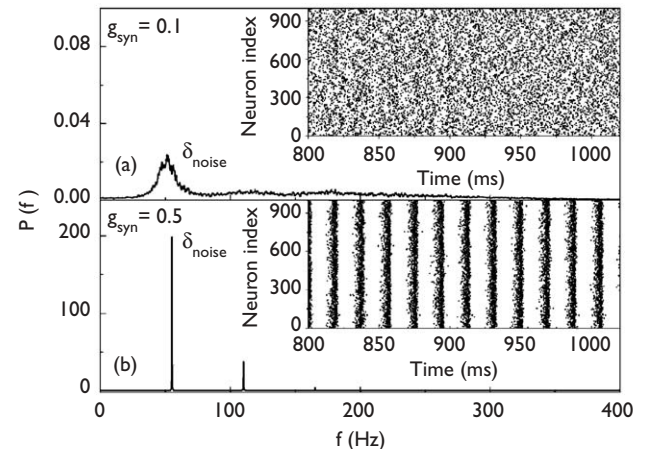
$$k = \frac{1}{N(N-1)} \sum_{i=1}^N \sum_{j=1, j \neq i}^N k_{ij}(\tau). \quad (9)$$

Thus,  $k$  quantifies the degree of neuronal synchronization in the network.

## RESULTS

**Generation of rhythmic oscillations:** When HH neurons are uncoupled, they are subjected to independent noisy inputs, and the output of such a network is characterized by asynchronous firings. The neuronal firing frequencies are around a main frequency, depending on noise intensity and intrinsic frequency of the neurons [15] (Fig. 1a). When neurons with spontaneous rhythmic firings are coupled together, synchronized firing will occur as long as the coupling strength among the neurons exceeds a critical value [15]. For example, for  $D = 5 \mu A^2/cm^4$  and  $g_{syn} = 0.5$  mS/cm<sup>2</sup>, there exists a high peak at 55 Hz in the PSD of  $V^*(t)$ , which is denoted by  $\delta_{noise}$  (Fig. 1b). This phenomenon, i.e., noise-induced synchronization transition via coherence resonance (CR) [14], has been studied in detail [15].

The frequency of such synchronized rhythm is determined by synaptic coupling strength  $g_{syn}$ , the noise intensity  $D$  and the intrinsic oscillation nature of the HH neuron [15]. When  $D$  varies from 1 to  $60 \mu A^2/cm^4$ ,  $f_{peak}$  increases from 45

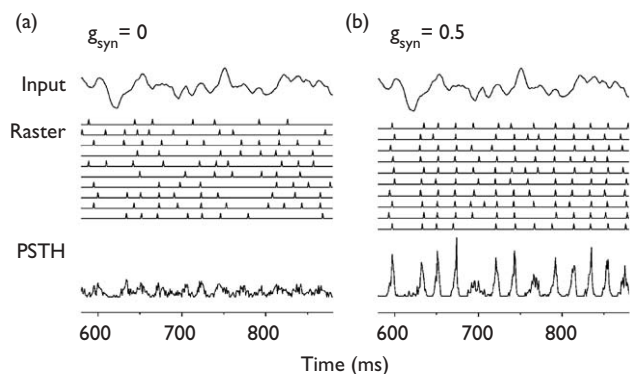


**Fig. 1.** PSDs of  $V^*(t)$  and the raster plots of firings of the neurons for  $D = 5$ , and  $g_{syn} = 0.1$  (a), 0.5 (b), respectively.

to 66 Hz for  $g_{syn}=0.1$  mS/cm<sup>2</sup>, while  $f_{peak}$  increases from 46 to 77 Hz for  $g_{syn}=20$  [15].  $f_{peak}$  tends to saturate for large values of  $g_{syn}$  and  $D$ . The frequency of the rhythmic oscillation of the network is mainly localized in the range of 40–80 Hz [15].

We have previously demonstrated the role of the synchronized rhythms in processing input periodic signals [15]. Each noise-free HH neuron has a frequency tuning property. The signals with preferred frequency can be easily detected by the neuron with relative low amplitude. The existence of noise can widen the tuning curve [20] by affecting the bifurcation dynamics. In the presence of noise, the network connection leads to spontaneous synchronous activities, which dramatically sharpens the frequency tuning curve to be narrower and stronger [15]. This greatly enhances the sensitivity of the network to periodic signal with preferred frequency. These effects result from the conventional nonlinear resonance between the rhythmic oscillation and periodic forcing of the signal, and the noise enhanced SR [15]. The resulting frequency tuning bands cross a large range of noise intensities, where large SNR ratio sustains, indicating that the signal processing is robust. This phenomenon suggests that various coherent rhythms in the working brain can serve as efficient information channel for processing periodic signals, which may be of biological significance.

**Information encoding of aperiodic signals:** Now we turn to investigate how these sustained synchronized activities affect the coding ability of neurons in the network to aperiodic signals. A subthreshold aperiodic signal  $s(t)$  is used as a test signal because it has richer structures and higher variability than a periodic one.  $s(t)$  is obtained by convolving a Gaussian white noise with a unit-area symmetric Hanning window filter with a fixed time constant. All the neurons are subjected to the same aperiodic signal  $s(t)$  (Fig. 2) plus uncorrelated noise. Neural behavior depends remarkably on noise intensity and synaptic strength. For  $D=5$  and  $g_{syn}=0$  mS/cm<sup>2</sup>, the responses of the network are highly imprecise even though many spikes



**Fig. 2.** (a) In the presence of noise  $D=5$ , the network with  $g_{syn}=0$  for input aperiodic stimulus  $s(t)$  (upper) displays noisy firing activities (see middle raster plot for 10 neurons). The peaks in the PSTH of total 1000 neurons (lower plot) are weak and random. (b) In the presence of noise  $D=5$ , the network with  $g_{syn}=0.5$  for input aperiodic stimulus  $s(t)$  (upper) displays ordered firing activities (see middle raster plot for 10 neurons). The peaks in the PSTH of total 1000 neurons (lower plot) are high and phase locked.

follow the variation of the stimulus  $s(t)$  (see raster plot in Fig. 2a).

The constructed post stimulus time histograms (PSTH) represents the coding activities of the network, which is weak and noisy. For  $g_{syn}=5$ , the spikes of the neurons become highly precise in time and are located near the peaks of the stimulus (see raster plot in Fig. 2b). The peaks in PSTH are stronger and smoother following the fluctuations of the signal. This suggested that strong coupling might lead to strong coherence among neuronal firings and more stable firing states in the noisy environment. To give a quantitative evaluation of coding property, we apply Shannon information theory [21] to the analysis of neural coding in the following.

Entropy is a quantitative measure used to quantify the ability of a coding scheme or a communication channel to convey information [21]. Here, each neuron in the network receive the same input signal  $s(t)$ . The spike trains of a studied neuron is  $r(t)$ . Thus, the total response entropy of each neuron can be described by

$$H(r) = - \sum_r P[r] \log_2 P[r]. \quad (10)$$

which is used to measure the theoretical capacity of any neuron in the network in conveying information. Mutual information  $I_m$  measures how much of that capacity is actually exploited to encode the signal,

$$\begin{aligned} I_m &= H(r) - H(r|s) \\ &= - \sum_r P[r] \log_2 P[r] + \sum_{s,r} P[s] P[r|s] \log_2 P[r|s], \end{aligned} \quad (11)$$

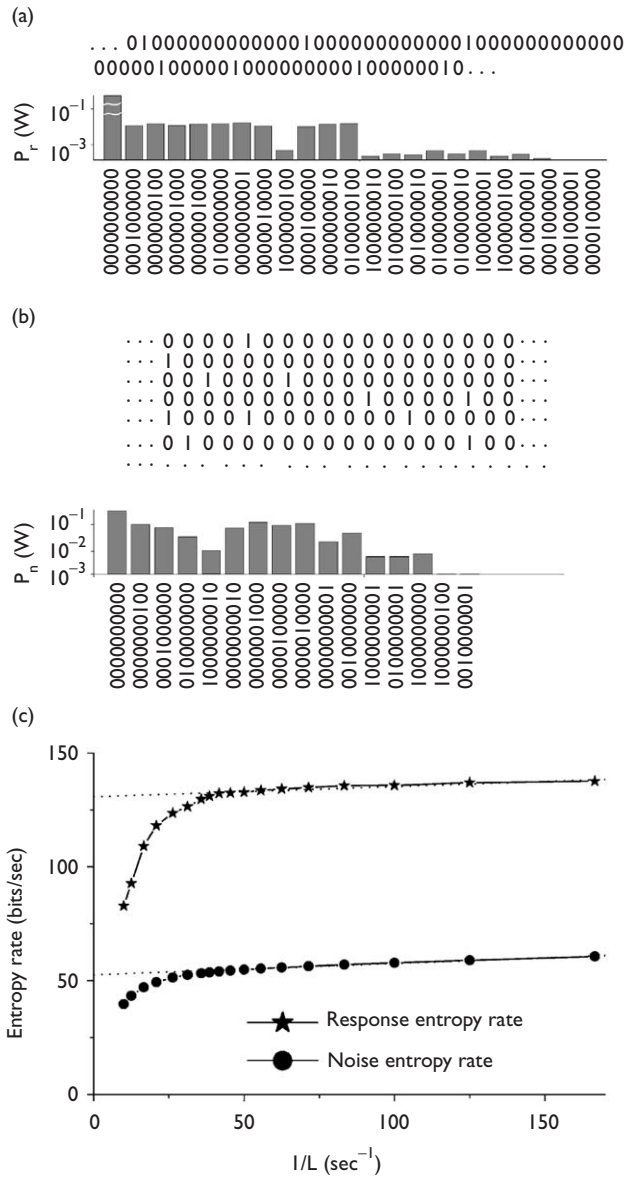
where  $H(r|s)$  can be define as noise entropy  $H_{noise}$  and is associated with that part of the response variability that is not due to changes in the stimulus but arises from other sources.

Here we follow Strong's direct method [22] to compute the mutual information and the total response entropy of individual neurons in the network. The spike train of a given neuron is first translated to a sequence of words. Each word  $W$  consists of  $L$  letters, while each letter has a time bin of  $\delta t=2$  ms. Thus, for a given spike train, we can compute the histogram of each possible word, which is used to represent the occurrence possibility of the word, i.e.,  $P[W(L, \delta t)]$ . Then, entropy can be computed by

$$H(L, \delta t) = - \frac{1}{L \delta t} \sum_W P[W(L, \delta t)] \log_2 P[W(L, \delta t)], \quad (12)$$

When we increase the size of the spike train,  $H(L, \delta t)$  will approach the real entropy of the spike train with such a distribution. An extrapolation value for infinite size is obtained to ensure the value of  $H(L, \delta t)$  approach to real one for given  $L$ . The response entropy  $H(r)=H_r(W)$  is computed in this way. Figure 3a shows an example how to compute the probability distribution of words with length  $L=10$  in one spike sequence, for the calculation of  $H_r$ .

The noise entropy  $H_{noise}$  which represents the variation of reproduced responses of a studied neuron in the network to the repeated stimulus, can be computed in the following way. For  $N$  repeated presentations of the stimulus, we get  $N$  trials of spiking responses. The histogram of words  $W$  at a particular time  $t$  can be computed to represent the probability of occurrence  $P_n[W|t]$ , which quantify the occurrence possibility of  $W$  in the repeated trials. Figure



**Fig. 3.** Illustration of calculation of mutual information rate. (a) Probability distribution of words  $P_r(W)$  of length  $L=10$  with time bin  $\delta t=2$  ms, for the calculation of  $H_r$ .  $P(W)$  for  $W=0000000000$  is far off scale (0.84). Although  $2^{10}$  patterns were possible, only 23 words actually occurred ( $n=50000$ ). Inset, samples of one sequence composed of different words. (b) Probability distribution of words  $P_n(W)$  of length  $L=10$  with time bin  $\delta t=2$  ms, at one time position in 500 repeated trials of one neuron, for the calculation of  $H_{noise}$ . Over 500 repeats, only 16 different words were observed. Inset, samples from 6 of the 500 trials to the repeated stimulus. A particular 10-bin word at time  $t$  is highlighted. (c) Estimated total response entropy rate  $H_r$  and noise entropy rate  $H_{noise}$  are plotted as a function of the reciprocal of word length,  $1/L$ . Both  $H_r$  and  $H_{noise}$  decrease gradually with increase of  $L$  implying of correlations between bins. The drop of the two curves for large  $L$  indicates the distortion effect due to the limited data. Dashed dotted lines show the extrapolations from the linear part of these curves to infinitely long words [22]. Mutual information is obtained by the difference between the two extrapolation values [22].

3b shows an example how to compute the probability distribution of words with length  $L=10$  in 500 repeated trials. Entropy for the distribution at time  $t$  is computed and then average over time to obtain the noise entropy,

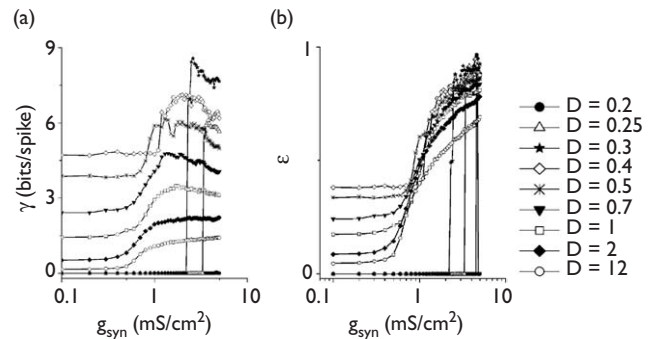
$$H_{noise} = \left\langle -\frac{1}{L\delta t} \sum_W P_n[W(L, \delta t)] \log_2 P_n[W(L, \delta t)] \right\rangle_t, \quad (13)$$

where  $\langle \dots \rangle_t$  denotes the average over all sampling times  $t$ . By increasing the number of trials, an extrapolation value is obtained for the noise entropy.

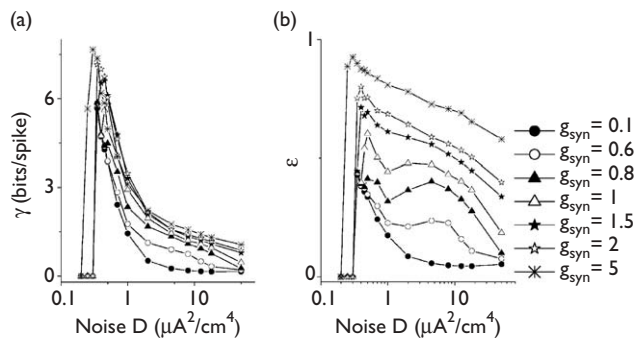
The extrapolation value of either the response or noise entropy is dependent on the word length  $L$ , as seen in Fig. 3c. However, we can estimate their values by extrapolating to infinite  $L$  [22]. Furthermore, we obtain mutual information by  $I_m = H_r - H_{noise}$ . (In the example shown in Fig. 3c,  $I_m = 130.75 - 52.25 = 78.5$  bits/s). The reliability of information transfer in neural encoding can be quantified precisely by two information measures: coding efficiency and information transmission rate [23]. The coding efficiency  $\epsilon$  is defined by  $\epsilon = I_m/H(r)$ , which quantifies the fraction of a neuron's activity that has been utilized to encode the signal. The information transmission rate ( $\gamma$ ), defined as the ratio of mutual information to mean firing rate, quantifies how efficient each spike carries information. Considering the difference among the neural responses in the network, we take an average over all neurons to obtain final results.

By changing the noise intensity  $D$  from 0 to 50 or coupling strength from 0 to 5, we obtain distributions of the information transmission rate  $\gamma$  and coding efficiency  $\epsilon$  for individual neurons in the network as a function of  $D$  or  $g_{syn}$  (Fig. 4, Fig. 5). It is worth noting that the information carried by each spike inside the neural activity, i.e., the information transmission rate  $\gamma$ , is maximized by some intermediate coupling strengths  $g_{syn}$  over a wide range of noise intensities (Fig. 4a). Given that the synchrony is a monotonous function of coupling strength, appropriate synchrony of the firings might be more appreciated in maximizing information transmission than that of stronger synchrony or asynchrony. Moreover, Fig. 4b indicates that the coding efficiency  $\epsilon$  is a monotonous function of coupling strength for different noise levels. This is reasonable because stronger coupling strength always leads to more robust state against noise.

In addition, for various coupling strengths, the information transmission rate  $\gamma$  and coding efficiency  $\epsilon$  varying with the noise intensity  $D$  demonstrate a classic aperiodic SR phenomenon [14] (Fig. 5). That is, information measures are maximized by optimal noise intensities, while the large noise intensity always tends to destroy the reliability of the neural response. The efficiency measure used here indeed reflects the ordering of the network against randomness. In



**Fig. 4.** (a) Information transmission rate  $\gamma$  as a function of coupling strength  $g_{syn}$  for various noise intensities. (b) Coding efficiency  $\epsilon$  as a function of coupling strength  $g_{syn}$  for various noise intensities.



**Fig. 5.** (a) Information transmission rate  $\gamma$  as a function of noise intensity  $D$  for various coupling strengths. (b) Coding efficiency  $\epsilon$  as a function of noise intensity  $D$  for various coupling strengths.

Fig. 5b, for  $g_{\text{syn}}$  around 1, there are two maxima as a function of noise  $D$ . The first peak derived from the maximal enhancement of phase locking of spiking response to the aperiodic signal by optimal noise intensity via SR. For the second peak, we can understand in the following. With the strong coupling, even in the absence of outer signal, there is an enhanced intrinsic order of the network with the optimal noise intensity via CR [15]. This results in a peak around  $D=5$  (Fig. 5b). For the stronger coupling strength ( $>1$ ), the forcing from the aperiodic signal become more dominant, so the peak induced by signal and noise via SR is prevailing, whereas the peak due to CR is weak relatively and even cannot be seen.

In this globally coupled network, coupling strength plays multiple roles. On the one hand, in the presence of noise disturbance, synaptic coupling increases the long-term correlation among spiking neurons, thus enhances the synchrony of neuronal spiking activities in response to stimulus. This suppresses the random firing variability induced by noise while preserves entrained spike responses by correlated signal common to all neurons. In this sense, increasing the coupling strength helps to increase the signal-related mutual information and decrease the noise entropy. On the other hand, strong synchrony tends to preserve the regularity of the network activity, and suppress any variability in spiking time. In this case, the network becomes inactive and insensitive to instantaneous variations in the signal, which indeed contain abundant information. The increase of the coding efficiency and robustness against noise is at the cost of decrease of sensitivity to the input transients. The tradeoff between these two forces results in an optimal synchronous state, where the information transmission rate and coding efficiency are maximized even in high noise levels.

## DISCUSSION AND CONCLUSION

Noise and synaptic coupling play important roles in optimizing the ordered state of the network activity in information transmission. Appropriate background noise can help neurons with synaptic connection generate spontaneous rhythmic activities in a network. Noise-induced rhythm, reflecting the natural frequency characteristic of the network, provides a frequency tuning mechanism for the network to process periodic signals efficiently in

noisy environments [15]. In this case, the stronger coupling is always advantageous in enhancing SNR.

The encoding process of aperiodic signals is different from that of periodic ones. Much stronger coupling enables the network with background noise to produce a more regular synchronous rhythm, which indeed suppresses heavily the sensitivity of the system to fast fluctuated signals. Also, regularity in the neural activity greatly increases the coding redundancy in information transmission. In a noisy environment, however, appropriate synchrony is beneficial in enhancing the information transmission and improving the coding fidelity against noise contamination. In order to obtain sufficient coding efficiency in information encoding process, increase of redundancy within certain limits is necessary and helpful. In addition, noise is not always deleterious. Optimal noise level can transfer some energy to the network and help detect the weak signals by SR. Our results indicate that it is not the weaker and stronger but an optimal synchronous state may be of functional significance in sensory process, with which the information encoding capacities of the network can be utilized maximally.

In this paper we only reveal one aspect of synchrony in information transmission in a globally connected network. In fact, experimental studies indicated that synchrony might be miscellaneous in information coding process [1–3]. It has been suggested that the precise spike timings relative to the synchronized oscillation may provide an additional temporal channel for encoding information [1,2,10]. This was supported by recent experiments by demonstrating that firing rate and spiking timing of the hippocampal neurons are dissociable and may encode two independent variables [24]. Learning-related synchronized oscillations plays a key role in synaptic plasticity, which was found to transform an asymmetric rate code into a temporal code [25]. Such a temporal coding scheme might be widely implemented in olfactory sensory neurons [1,2], hippocampal neurons [24,25], and other sensory neurons [1,2]. In hippocampal cultures, most of the spontaneous spikes are triggered by synchronously arriving excitatory synaptic input, suggesting a privileged role of synchronized activity in synaptic information transmission [11]. In the future work, complex forms of coupled networks are expected to investigate the role of the synchrony spikes among different layers in the coding of spatial image and temporal signals. The kind of information carried by firing rate or spike timing in the coding process needs to be further clarified.

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